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FURTHER OBSERVATIONS ON THE CAUSE OF THE COMMON DRY-ROT OF THE POTATO TUBER IN THE BRITISH ISLES.

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(PLATES VI–VII.)

[*Authors alone are responsible for all opinions expressed in their Communications.*]

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XXI.

FURTHER OBSERVATIONS ON THE CAUSE OF THE COMMON DRY-ROT OF THE POTATO TUBER IN THE BRITISH ISLES.

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(Plates VI.–VII.)

[Read February 27. Published June 12, 1917.]

I.—Introductory.

In a previous paper communicated to this Society and published nearly nine years ago[1] it was shown that the dry-rot of the potato tuber was due to a parasitic species of Fusarium which was then regarded as being *F. Solani* Sacc.

The object of that paper was to record evidence to show that this form of rot was in reality due to the Fusarium fungus, and to it alone, without the co-operation or intervention of bacteria or of other micro-organisms, which some previous authors held to be necessary to establish the rot. Since that time there has been no more controversy on this point.

It was assumed by the authors of that paper (as also by several previous authors, including Pizzigoni and Wehmer) that *Fusarium Solani* Sacc. was the correct name of the fungus which caused the rot. But beyond obtaining pure cultures of the fungus for the purpose of inoculation, no cultural or morphological studies of it were undertaken at that time, and no critical attention was paid to the actual identity or nomenclature of the fungus.

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[1] Pethybridge, G. H., and E. H. Bowers. Dry-rot of the Potato Tuber. Econ. Proc. Roy. Dublin Soc., vol. i. Part 14, August 1908, p. 547.

Recent investigations of the genus Fusarium, particularly those of Appel and Wollenweber,[1] have, however, shown that very great confusion prevails in the ealier literature as to what fungus is really and correctly represented by the name *Fusarium* (*Fusisporium*) *Solani*. It appears that the specific name *Solani* has been applied at one time or another to no less than nine distinct species of this genus; and even the original *Fusisporium Solani* of Martius proves to be a name which includes two distinct species, and these Appel and Wollenweber name *Fusarium Solani* (Martius pro parte) and *Fusarium Martii* (n. sp.).

This being so, it seemed eminently desirable to make a renewed study of the fungus causing the dry-rot of the potato in this country, with a view to ascertaining its exact identity, and whether only one species commonly causes the rot. This was all the more necessary in view of the fact that this disease of the potato has received an increasing amount of attention on the part of phytopathologists in recent years, notably in the United States of America; and it was important to know whether the prevalent dry-rot-producing organisms were identical on the two continents.

Before dealing with the further investigations which we have made concerning the disease, it is necessary to give a review of the literature on the subject which has been published since the appearance of the previous paper in 1908.

II.—Previous Literature.

In 1909 Miss Longman[2] published a description of the disease as it occurs in the south of England. Two types of fungus pustules are described as occurring on naturally affected tubers, viz.:—(1) those consisting of small tufts of hyphae bearing typical Fusarium conidia, usually white or buff-coloured, but sometimes pink; and (2) those in which the conidia are at first enclosed in a structure having a thin wall made up of closely interwoven hyphae, this wall being sometimes buff-coloured, but more often pink. Some of these structures possess no openings, but others have an apical pore, and are regarded by Miss Longman as being pycnidia. Owing to the production of these structures, the authoress proposed to remove the fungus from the genus Fusarium and place it in that of Aschersonia Mont.

Miss Longman states that if potatoes affected with dry-rot are not wholly

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[1] Appel, O., and H. W. Wollenweber. Grundlagen einer Monographie der Gattung Fusarium (Link). Arb. Kais. Biol. Anstalt, Bd. viii. Heft 1, 1910.

[2] Longman, S. The Dry-rot of Potatoes. Journ. Linn. Soc., vol. xxxix. Bot. ix. 270 1909, p. 120.

killed before the spring, the eyes on the sound parts of the tubers may sprout in a normal way; but as soon as the disease reaches the shoots, the latter shrink at their bases, their leaves blacken and they die. Nothing definite can be gleaned from Miss Longman's field infection experiments, since the plants in the uninoculated and control plots showed as much disease as those in the inoculated plots.

From the description and rather poor figures of the fungus given by Miss Longman, and referred to as *F. Solani*, it is difficult to decide with certainty which species was being dealt with. On the whole, it seems not improbable that the fungus was *F. cæruleum*. In our work with this species, however, we have failed to observe the "pycnidia" described by Miss Longman.

In England the dry-rot of the potato (or "Winter-Rot," as it has also been called there) was stated in 1904 by Massee[1] to be caused by *Nectria Solani* Pers., a name unfortunately adopted subsequently in official publications in that country. This name, however, is not traceable to Persoon, but to Reinke and Berthold,[2] and when this was realized the revised name *Nectria Solani* Reinke and Berthold was substituted in these publications. It is certain, however, that the fungus causing the dry-rot of the potato has nothing whatever to do with *Nectria Solani* Reinke and Berthold, an organism which these authors themselves showed to be a mere saprophyte, and to have a conidial form resembling not a Fusarium but a Spicaria.

Probably led astray by these official but erroneous publications, Eriksson[3] also wrongly ascribed the dry-rot of the potato to *Nectria Solani* Reinke and Berthold, while Evans,[4] probably similarly misled, ascribed it to *N. Solani* Pers. The same source doubtless accounts for the similar error made by Lounsbury.[5] The kind of evidence presented at a later date by Massee,[6] purporting to establish a connexion between *Nectria Solani* R. and B., Fusarium and various other fungi is quite inadequate to do so, or to show that any of them cause dry-rot.

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[1] Massee, G. Some Diseases of the Potato. Gardeners' Chronicle April 24th 1904, p. 257.

[2] Reinke, J., and G. Berthold. Die Zersetzung der Kartoffel durch Pilze. Berlin, 1879, p. 39.

[3] Eriksson, J. Hvitrota och Kräfta å potatis. Centralanstalten för Jordbruksförsök, Flygblad 8, Feb. 1909.

[4] Evans, I. B. P. Potato Rot (*Nectria Solani* Pers.). Transvaal Agric. Journ., vii. 25, 1908, p. 64.

[5] Lounsbury, C. P. Dry-rot of the Potato. Agric. Journ. Cape of Good Hope, xxxv. 1909, p. 42.

[6] Massee, G. Diseases of Cultivated Plants and Trees. London, 1910, p. 182.

Turning now to the work of American investigators, it is necessary first to recall that of Smith and Swingle[1] published in 1904.

These authors regarded the rot of the tuber as being caused by *Fusarium oxysporum* Schlecht, this name being taken to be a synonym of *F. Solani* Sacc. A perusal of their account of the disease shows at once, however, that their form of rot differs in several essential points from the common dry-rot of the tuber, as we know it here; and they were apparently in error in supposing that the type of dry-rot described by European authors was identical with that studied by them. In Smith and Swingle's form of dry-rot the infection of the tuber is stated to occur normally at its heel end, through the diseased rhizome; and the subsequent decay of the tuber is stated to proceed from the region of the ring of darkened vascular tissue.

Further, Smith and Swingle's disease does not consist merely of a dry-rot of the tuber, but is one in which all of the underground parts of the plants may be attacked and killed, with the result that the overground portions also succumb, although the mycelium of the fungus does not penetrate upwards into the aerial stems. It is rather a disease of the potato plant as a whole, than merely a dry-rot of the tubers.

Some years later Manns[2] published an account of a similar disease, in which the plant becomes infected at its roots, and the tubers through their rhizomes. This author proved to his own satisfaction, by means of cultures, that the fungus which produced the wilt of the plant was identical with that which caused the subsequent rotting of the tubers during storage. He used for it the name *Fusarium oxysporum* Schlecht, but stated at the same time that he was quite aware that the name *Fusarium solani* was commonly used for it.

It is quite clear that Smith and Swingle, as well as Manns, concluded that the storage-rot of the tubers was caused by the same fungus as that which also produced the "wilt" disease of the growing plant (*Fusarium oxysporum* Schlecht). It seems, however, that they may have been mistaken in this matter. According to Wollenweber[3] the American *Fusarium oxysporum* Schlecht causes the wilt of growing potato plants, but only uses the xylem of the stem-end of the tubers for over-wintering, without producing a rot of the parenchyma. Further, after giving a morphological diagnosis of this species, this author states that it is a "vascular parasite, cause of wilt

[1] Smith, E. F. and D. B. Swingle. The Dry-rot of Potatoes due to *Fusarium oxysporum*. Bull. 55. Bureau of Plant Industry. U.S.A. Dept. of Agric., 1904.

[2] Manns, T. F. The Fusarium Blight (Wilt) and Dry-Rot of the Potato. Bull. 229. Ohio Agric. Exp. Station. Wooster, 1911, p. 299.

[3] Wollenweber, H. W. Studies on the Fusarium problem. Phytopathology. vol. iii. No. 1. Feb. 1913, p. 24.

disease, but not tuber-rot, of *Solanum tuberosum* in the United States of America, possibly also in Southern Europe, and the potato districts of South Africa, Australia, &c."

Quite a different type of dry-rot was described by Jamieson and Wollenweber in America[1] about four years ago, which, in its general aspects, much more closely resembles the common dry-rot of potato tubers in our own country, although it differs from the latter in some respects, as will be shown later (see p. 218). These authors state that this new form of dry-rot is clearly to be distinguished from the wilt and dry-rot ascribed by Smith and Swingle to *F. oxysporum*; and, presumably to emphasize this distinction, they refer to the new form as an *external* dry-rot. The cause of it was determined to be a new species of Fusarium to which the name *F. trichothecioides* was given. It is stated that tubers could be infected with the disease by merely rubbing their surfaces with a platinum loop bearing the fungus, although more certain results were obtained when the inoculation was made through an actual wound.

It is important to know whether this species not only rots tubers, but also causes a wilt of the plant, as *F. oxysporum* does. Apparently Jamieson and Wollenweber believe that it does cause a wilt, although they do not seem to be absolutely confident in the results of their experiments, for they do not include this important point in the summary which they give of their work.

What at first sight, at any rate, would appear to be yet another American type of dry-rot of the potato tuber was described in 1913 by Wilcox, Link, and Pool.[2]

Although in a general way this rot appears to be similar to the external dry-rot described by Jamieson and Wollenweber, yet the organism causing it was considered by the three authors to be a new one, and they named it *Fusarium tuberivorum*. They distinctly state that the fungus is incapable of infecting any part of the potato plant other than the tuber, hence it is not a wilt-producing parasite, and in this respect, therefore, it must be regarded as clearly differing from *F. trichothecioides*, if Jamieson and Wollenweber's views on this matter are correct.

Soon after the publication of Wilcox, Link, and Poole's description of *F. tuberivorum*, Wollenweber[3] stated that he, in common with Orton and

[1] Jamieson, C. O., and H. W. Wollenweber. An external Dry-Rot of Potato Tubers caused by *Fusarium trichothecioides* Woll. Washington, Academy of Science ii. No. 6, 1912, p. 146.

[2] Wilcox, E. M., Link, G. K. K., and V. W. Pool. A Dry-Rot of the Irish Potato Tuber. Research Bull. No. 1. Nebraska Agric. Expt. Station, 1913.

[3] Wollenweber, H. W. Ramularia, Mycosphaerella, Nectria, Calonectria, usw. Phytopathology. vol. iii. No. 4. 1913, p. 206.

Jamieson, regarded this species as being identical with the subnormal stage of *F. trichothecioides.* But if these two species be identical, it is difficult to see why one of them (*F. trichothecioides*) should cause a wilt of the potato plant and the other one (*F. tuberivorum*) should not do so.

To some extent this discrepancy may, perhaps, be regarded as explained by results obtained by Link,[1] and published in a paper which reached us whilst the present paper was in preparation for press. Link states that he agrees that *F. tuberivorum* Wilcox and Link is the same species as *F. trichothecioides* Woll. Contrary to what was stated in his previous paper, he now states that this species *is* capable of producing a wilt of the potato plant as well as a rot of the tuber, and further he shows that, contrary to Wollenweber's opinion, *F. oxysporum* is not only a wilt-producing organism, but does also cause a rot in tubers. In other words, both *F. oxysporum* and *F. trichothecioides* can produce both tuber-rot and wilt of the potato plant; but, according to Link, under field and storage conditions respectively, the former is more probably responsible for wilt, and the latter for tuber-rotting.

Pratt[2] describes the rot due to *F. trichothecioides* as a "powdery dry-rot," and states that it is apparently restricted to the arid and semi-arid sections of the western part of the United States. He agrees that *F. tuberivorum* is identical with *F. trichothecioides,* but, working with this fungus under western field and laboratory conditions, he states that he failed to produce an infection in any part of a growing potato plant. His results, therefore, are contrary to those of Jamieson and Wollenweber, agree with those of Wilcox, Link, and Pool, but differ from those of Link subsequently published.

Two further types of dry-rot have been described in America by Carpenter.[3] One, called a "stem-end and wound-invading dry-rot," was found to be caused by a new species of Fusarium for which the name *F. eumartii* was proposed. The second, similar in type to the first, is caused by *F. radicicola* Wollenw. This author refers to the so-called "jelly-end" rot, which, he says, is a serious trouble in California, and he finds *F. radicicola* and *F. oxysporum* associated with it. Carpenter agrees with Smith and Swingle (and with Link), but differs from Wollenweber in ascribing to *F. oxysporum* the power of causing tuber-rot. *F. hyperoxysporum* Woollenw. was also proved to be capable of producing a tuber-rot.

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[1] Link, G. K. K. A physiological study of two strains of Fusarium in their causal relation to tuber-rot and wilt of potato. Bot. Gaz. lxii. No. 3. 1916, p. 169.

[2] Pratt, O. A. Control of the Powdery Dry-Rot of Potatoes caused by *Fusarium trichothecioides.* Jour. Agric. Research. vol. vi. No. 21. 1916, p. 817.

[3] Carpenter, C. W. Some potato tuber-rots caused by species of Fusarium. Journ. Agric. Research. v. No. 5. 1915, p. 183.

Pratt[1] calls the rot due to *F. radicicola* "a field black-rot," and states that this fungus is capable of causing a jelly-end rot, but that under field conditions other factors are in part responsible. Both black-rot and jelly-end rot appear to be field rather than storage rots.

Haskell[2] isolated *F. eumartii* from tubers affected with a heel-end form of dry-rot in New York, and he proved as the result of pure culture inoculations that this species was capable of producing not only a wilt of the plant but also a rot of the tuber.

It will be clear from what has been said that considerable attention has been devoted during recent years in the United States of America to the various types of potato tuber dry-rot found there, but further critical study is necessary to clear up the important discrepancies which at present appear to exist between the results obtained by the various authors.

Before concluding this survey it is necessary to refer briefly to certain recent publications which deal with the question of the pathogenicity of some of the better known species of Fusarium towards the potato.

Wollenweber & Schlumberger[3] maintained in 1911 that, of the five species—*F. Solani* (Mart.) A. & W., *F. cæruleum* (Lib.) Sacc., *F. orthoceras* A. & W., *F. subulatum* A. & W., and *F. discolor* A. & W., all were incapable of causing a rot in tubers. In the case of the first two species, however, the conidia used for inoculation did germinate within the tubers and caused some local decay which did not spread, and in no case led to the rot of the whole tuber.

In a later report[4] from the same institution it is stated that preliminary infection experiments with species of Fusarium had shown that *F. discolor* var. *sulphureum* (Schlecht) and *F. cæruleum* (Lib.) were the species which most energetically attacked the tuber. *F. subulatum* App. & Wr. and *F. rubiginosum* App. & Wr. did so to a less degree, while *F. Solani* (Mart.) App. & Wr., *F. Martii* App. & Wr., and other species, gave negative results. Further trials showed that *F. discolor* var. *sulphureum* was distinctly the most active parasite, followed by *F. subulatum*, *F. metachroum* and *F. cæruleum*. Nine other species are mentioned which caused some damage to inoculated

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[1] Pratt, O. A. A western field-rot of the Irish potato tuber caused by *Fusarium radicicola*. Journ. Agric. Research. vi. No. 9. 1916, p. 297.

[2] Haskell, R. J. Potato wilt and tuber-rot caused by *Fusarium eumartii*. Phytopathology. vi. No. 4. 1916, p. 321.

[3] Wollenweber u. Schlumberger. Infektionsversuche mit kartoffelbewohnenden Pilze. Mitt. K. Biol. Anstalt f. Land u. Forstwirtschaft. Heft. 11. 1911, p. 15.

[4] Appel u. Fuchs. Zur Kenntniss der Fusariumfäule der Kartoffeln. Mitt. K. Biol. Anstalt, Heft 14. 1913, p. 16.

tubers when the latter were kept at rather high temperatures, viz. from 27° C. to 33° C.

In his most recent paper[1] Wollenweber mentions eight species of Fusarium as being capable of rotting potato tubers. Tho four most important species in this respect are stated to be:—

(1). *F. cæruleum* (Lib.),
(2). *F. discolor* var. *sulphureum* (Schlect.),
(3). *F. trichothecioides* Wr.,
(4). *F. ventricosum* App. & Wr.,

for all of them are capable of producing total destruction of tubers when inoculated through artificial wounds.

Of the other four *F. orthoceras* App. & Wr. is said to be the probable cause of the jelly-end rot of the potato tuber; *F. rubiginosum* is a wound parasite on cereals, and is also found on potato tubers, where it is less active than the first three species mentioned above. *F. gibbosum* is said to be a probable cause of potato tuber-rot, but the results of infection experiments were not so uniformly positive as in other species. *F. subulatum* is parasitic only under conditions of high humidity and restricted air supply, and is less active than *F. cæruleum* and others.

It will be observed that unanimity between the various authors does not always prevail. Our experience leads us to believe that, in studying the pathogenicity of the various species of Fusaria towards the potato tuber, there are certain factors which have a very considerable influence on the results which may follow inoculation. These are—(1) the variety of the tuber; (2) its condition of maturity; (3) the length of time that the fungus used for inoculation has been in purely saprophytic culture, and (4) the prevailing temperature and moisture conditions. In comparative tests of pathogenicity these factors should as far as possible be identical.

Finally, reference must be made to the most recent study of the various species of Fusarium associated with decaying potato tubers, namely, that of Sherbakoff,[2] who describes no less than sixty-one species and varieties, including all those already mentioned in the present paper. This author's work consists, in the main, of a description of the various species and varieties of Fusarium, according to their morphological and cultural characters; but

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[1] Wollenweber, H. W. Studies on the Fusarium problem. Phytopathology. vol. iii. No. 1. Feb. 1913, p. 24.

[2] Sherbakoff, C. D. Fusaria of Potatoes. Cornell. Univ. Agric. Expt. Station. Memoir No. 6. 1915.

a certain amount of attention is also devoted to the question of the pathogenicity of the different species towards the potato. Inoculations of potato plants with all of the species described gave negative results as far as wilt production was concerned, but the author does not conclude that all of these species are incapable of producing wilt, given the proper conditions. Inoculations of tubers showed that a considerable number of the species caused more or less rapid decay, and that most of them only readily caused rotting after the tubers had begun to sprout. The commonest rot-producing organism, at least in the eastern United States, is said to be *F. cæruleum* (Lib.) Sacc.

It is stated[1] that this organism was isolated repeatedly from diseased tubers, and every strain isolated proved capable of producing more or less dark-coloured dry-rot in tubers. Further, Sherbakoff states that a white-rot of tubers is produced by *F. lutulatum* and some of its allies, a distinctly striate rot by *F. striatum*, a brownish rot by *F. trichothecioides*, and a more or less pinkish rot with large cavities by *F. subulatum* and its variety *brevius*. Of all these *F. cæruleum* is stated to be the commonest and most vigorous wound parasite of potato tubers, the next perhaps being *F. subulatum*, and its variety *brevius*.

It is apparent from a review of the literature that the potato tuber is capable of being destroyed by several totally distinct species of Fusarium, and that in most cases the decay is of the nature of a dry-rot. It is also clear that some of these species may produce a "wilt" of the potato plant. Our object was therefore to find out whether one or more of these species, and if so which of them, was responsible for our common dry-rot, and to ascertain whether the species concerned also caused a wilt-disease of the plant.

III.—Investigation Work.

The investigations dealt with in the present paper have been in progress, concurrently with studies of other potato diseases, during the past three or four years.

Naturally, much of the diseased material examined has been of Irish origin, but we have also been fortunate in securing for detailed investigation a number of characteristic specimens of the disease from England and Scotland[2] sufficient to lead us to believe that there is but one commonly occurring form of dry-rot affecting potato tubers in the British Isles.

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[1] loc. cit. p. 261.

[2] We desire to express our thanks to Mr. A. D. Cotton, of Kew; to Mr. E. S. Salmon, of Wye; and to Dr. W. G. Smith, of Edinburgh, for their kindness in providing us from time to time with supplies of typically diseased material from England and Scotland.

Cause of the Rot.—We may at once anticipate the general conclusion at which we have arrived as a result of our studies by stating here that the fungus which we have found to be the cause of our common dry-rot is *Fusarium cæruleum* (Lib.) Sacc., and that although it does directly cause the decay of potato tubers, it does not produce hadromycosis (wilt) of the plant, such as is produced by *Verticillium albo-atrum*,[1] and, according to some authors, by certain species of Fusarium. Nor do we believe that it causes a disease of the potato plant by attacking the roots.

This species has been recognized on the Continent of Europe since the beginning of the nineteenth century, but has not usually been regarded as a definite parasite. Saccardo[2] records it as occurring in putrid tubers, and Rabenhorst[3] on rotting potatoes. More recently Appel and Wollenweber[4] in Germany state that it is a comparatively rare species on potato tubers; and these authors suggest that this may perhaps be accounted for by its slow growth when compared with other species such as *F. solani*. This does not necessarily conflict with our view that *F. cæruleum* is the species commonly causing dry-rot, for the tubers examined by these authors were evidently not merely those which had been destroyed by dry-rot, but must also have included many killed by *Phytophthora infestans*, parasitic bacteria, &c., on which various saprophytic species of Fusarium subsequently flourish.

Not nearly so much attention has been paid in America to this species as to *F. oxysporum*, *F. trichothecioides*, and others, although (as previously mentioned), according to Sherbakoff, *F. cæruleum* is the commonest rot-producing Fusarium in the United States, at any rate so far as the eastern States are concerned.

As a British fungus the species is recorded by Massee,[5] who gives an extremely brief description of it, and states that it occurs "on rotten tubers of potato," thus suggesting rather a saprophytic than a parasitic habit. In British phytopathological literature the species is conspicuous by its absence from mention. We cannot now be certain on the point, but a re-examination of the fungus present on affected tubers, preserved both dry and in spirit from the time of our 1908 paper, leads us to suspect strongly that what we then called *F. solani* was in reality *F. cæruleum*.

Eleven distinct cases of the disease have carefully been studied by us.

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[1] Pethybridge, G. H. The Verticillium Disease of the Potato. Sci. Proc. Roy. Dublin Soc. xv. (N.S.) No. 7. p. 63. March 1916.

[2] Saccardo. Syll. Fung. iv. 1886, p. 705.

[3] Rabenhorst. Kryptog. Flora, I. 9, p. 574.

[4] Loc. cit. p. 84.

[5] Massee, G. British Fungus Flora. vol. iii. 1893, p. 481.

In each of them *F. cæruleum* was proved to be the cause of the rot, and eleven strains of the fungus have been isolated, and studied in very considerable detail. Except for slight variations in their relative degrees of pathogenicity, these strains have proved to be identical with each other, and also with a strain of *F. cæruleum* procured from the Central Bureau of the International Association of Botanists in Amsterdam.

Two further cases of the rot were met with when our cultural work was nearly completed; and in these cases also it was proved that the fungus responsible for the decay was *F. cæruleum.*

Occurrence of the Disease.—The most serious cases of the disease have usually been met with in seed tubers of early varieties such as May Queen and Ninety-fold, but it is by no means confined to such varieties. Complaints regarding it are more commonly made in the early months of the year than in the autumn, and this is probably correlated with the fact (to be discussed later) that the maturity of the tuber has a good deal to do with the incidence of the disease. We have never observed a case of the disease on tubers still attached (as they are in summer and early autumn) to the parent plants, nor have we seen it at the time of digging. The rot is essentially a storage one, the visible effects of which are seen during the winter, and particularly in the early spring.

Description of the Rot.—The rot may begin in any external region of the tuber, and is not associated with the heel or stem-end more than with any other part. It very frequently originates at obvious wounds or lesions of the skin, but often such injuries are not apparent where infection has occurred, and, as will be shown later (see p. 213), infection can occur in the absence of damage of this kind. A single tuber may be affected in several distinct regions at one and the same time, but as time progresses the decayed regions approach one another, and ultimately coalesce.

In the earliest visible stages of attack the skin becomes somewhat darker in colour than usual, and is slightly sunken. As time goes on the diseased area spreads, the sunken dark skin becomes folded or ridged into more or less parallel or concentric wrinkles, while fungus pustules break out through it. During this time the rot also penetrates more deeply into the inner tissues of the tuber. (See fig. 1, Plate VI.)

The rot as a rule proceeds until the tuber is entirely destroyed. During its progress much water is lost, the tuber shrinks, and finally becomes light in weight, dry, and quite hard. In this condition it is quite difficult to cut it with a knife. (See fig. 2, Plate VI.)

If a partially rotted tuber be cut open, it will be observed that the older decayed tissues are rather dry and brown in colour, but the browning has

no special association with the "vascular ring." Affected tubers often show a few cavities more or less completely filled with mycelium, which, however, as a rule, does not in these circumstances bear many conidia or chlamydospores. The newly killed tissues are still moist, more or less yellowish in colour, and of a granular consistency. The line of demarcation between the diseased and healthy tissues is not always strongly marked when an affected tuber is first cut open, but on standing exposed to the air the diseased portion gradually becomes distinctly browned.

In the interior of a completely rotted tuber, cavities containing a luxuriant growth of mycelium are also present. The mycelium lining the walls of these cavities is frequently distinctly blue ; and very often this colour also pervades the dead tissues for some little depth around the cavities. The intervening portions of the dead tissues are, at this stage, of a dirty white colour, and are more or less easily reduced to powder on being rubbed between the fingers.

Microscopical examination of sections made at the junction of the diseased and healthy tissues reveals the presence of branched, septate mycelium between the cells of the diseased tissues. In the completely browned and nearly dry, dead tissues, however, the mycelium is found to be both intra- as well as intercellular. The starch grains remain unattacked.

The fungus pustules present on the wrinkled skin are not arranged in any definite order or system, nor are they all absolutely alike, either as regards shape and size or colour. They are, as a rule, white on their surfaces; but if the outer layers be rubbed or scraped away, or if the pustules be sectioned, their bases are seen to be deep blue in colour. Occasionally the pustules are superficially blue, while they may also be distinctly pink, especially if the rotting tubers have been exposed to a good light.

The base of each pustule is made up of a compacted mass of hyphae running more or less at right angles to the surface of the tuber, and blue in colour. From this base a very large number of branched *conidiophores* bearing septate, fusiform conidia arise. The conidiophores are illustrated in fig. 1, Plate VII. The ultimate branches of the conidiophores (sterigmata) are somewhat swollen, more or less fusiform cells. At the apex of each sterigma, after the first and each subsequent conidium has been formed, there remains a not-easily-discerned, slightly funnel-shaped, projecting, empty sheath or collar, formed from the cell-wall at the point where the first conidium and the sterigma part company.

The base of each succeeding conidium remains for a longer or shorter period within this sheath, and, doubtless, it is this fact (as we found Appel

and Wollenweber had already suggested) which gives rise to the foot-like shape sometimes exhibited by the basal-cells of the conidia.[1]

The conidia produced on the pustules are slightly sickle-shaped and rather bluntly pointed at both ends. In general shape they somewhat resemble that of a pea-pod; and, just as the latter is enclosed at its base by the persistent calyx of the flower, so the base of the conidium rests within the sheath, as described above.

Typical conidia are shown in fig. 2, Plate VII. When produced in great quantities, under moist conditions, the conidia form rather slimy masses on the surfaces of the pustules. The conidia on the pustules are usually from 0- to 3-septate; i.e. from 1- to 4-celled; but the 3-septate forms always predominate. (In cultures 5- and 6-celled conidia are also produced.) In size they vary considerably, according to the conditions of moisture under which the tuber is decaying. The averages (in microns) for the various forms are as follows:—

0-*septate.*	1-*septate.*	2-*septate.*	3-*septate.*
14 × 3·7.	19 × 4·1.	21 × 4·3.	27 × 4·8.

In healthy artificial cultures the conidia produced are generally somewhat larger than those found on the pustules.

The *chlamydospores,* which occasionally occur on the pustules, are more or less spherical, possess somewhat thick, smooth walls, and are blue in colour. They are produced singly, in pairs, in chains, or in irregular groups. Their average diameter is 8 to 9 μ. Chlamydospores are shown in figs. 4 and 5, Plate VII.

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[1] It may, perhaps, be pointed out that the explanation of the origin of this "foot" structure of the basal cell of the conidium given by Wilcox, Link and Pool (*loc. cit.* p. 23) does not appear to be correct. The figures on which the explanation given by these authors is based are of hyphae, and not of conidia. If their explanation is correct, both the apical and the basal cells of a conidium should show the "foot"; but we have not found this to be the case.

The sterigma-sheath is clearly illustrated by Sherbakoff (*loc. cit.* p. 129, fig. J) for *F. cuneiforme,* but its significance is not alluded to. We have found that the foot-like appearance of the basal cell is most strongly developed in old and nearly-exhausted cultures, in which conidia are produced only slowly. In such cases the extremity of the basal cell must remain confined within this sheath for a considerable time, while the part immediately beyond it is free to expand. Since the conidium seldom sits symmetrically in this sheath, the small heel-like swelling usually occurs only on one side, and thus gives the foot-like appearance to the basal cell.

Seeing that the shape of this basal cell is, therefore, dependent on conditions of growth or culture, too much stress must not be laid on it as a morphological character for any particular species. In *F. cæruleum* it is not usually a very marked character, and frequently it is entirely absent.

Germination of the Conidia.—In hanging drops of rain-water ripe conidia germinate within a few hours. The individual cells of the conidium first become swollen, and it thus becomes somewhat constricted in the regions of the septa. Germ tubes may arise from any or all of the cells of a conidium. No fragmentation of the conidia into their constituent cells with a subsequent rounding off, previous to germination, as described by Smith[1] for *Fusisporum Solani* Mart., has been observed by us in *F. cæruleum*. Germinating conidia are shown in fig. 3. Plate VII.

Isolating the Fungus.—In no group of fungi is it more essential than in the genus Fusarium that the starting-point of a pure culture should be a single conidium, and we used this method. There is no particular difficulty in the matter in this case, seeing that the spores are large; and isolated individuals can, with comparative ease, be found and kept under observation under the microscope, on poured plates of suitably diluted conidia-suspensions. Thence transference singly to media in tubes is not a matter of real difficulty to a skilled worker. Appel and Wollenweber found the isolation of this species difficult, but that is probably because the material from which they started was a more or less heterogeneous mixture of the various kinds of organisms found associated together on rotten potatoes, and was not, as in our case, a pustule produced on the surface of a tuber in the comparatively early stages of a definite dry-rot.

If diseased material in not too advanced a stage of decay is available, it is also a comparatively easy matter to obtain cultures by removing, under aseptic conditions, small portions of tissue from the junction between the still healthy and the diseased portions of the tuber, and placing them on suitable nutrient media. Many of such cultures, if prepared with skill, will be found to be pure; others will become contaminated with stray germs during preparation. Failing diseased material in just the right condition it can be prepared by first inoculating a previously externally-disinfected, healthy tuber from a conidial pustule, and, when the rot has proceeded sufficiently far, by removing small portions of tissue, as described, to suitable media. For critical work, of course, this method is not admissible. Nevertheless, we have found that in the case of *F. cæruleum*, at any rate, a considerable proportion of the cultures thus obtained are pure.

Growth in Pure Cultures.—The fungus has been cultivated on more than a dozen different media, but they have not all proved equally suitable.[2] The

[1] Smith, Worthington G. *Diseases of Farm and Garden Crops.* London. 1884. p. 31.

[2] It should be stated that in none of our cultures have any forms of fructification other than conidia or chlamydospores been developed, although we have been successful in obtaining the development of perithecia *in vitro* with pure cultures of *Hypomyces Solani*, *Nectria Rubi*, and with one or two other fungi.

best of those used were Quaker Oat agar, oat extract agar,[1] slices of cooked potato tuber, and cooked potato stalks. In all cases where gelatine media were used, the fungus caused liquefaction of the gelatine. On the four media mentioned the fungus grew well, developed both conidia and chlamydospores, and exhibited the characteristic blue coloration which its specific name implies. When grown on ordinary beef-extract agar or gelatine, or on potato-juice gelatine, the colour was not produced, and chlamydospores were absent. The colour was, however, produced in cultures on beer-wort gelatine, but here, again, no chlamydospores were developed.

On Quaker Oat agar the growth is at first white. Later on the medium which the mycelium permeates becomes claret-coloured, while the aerial mycelium shows all stages of colour, from white to claret and blue. The conidia are borne in more or less slimy or viscous masses on the surface of the medium, and these masses vary in colour, from dirty white, through cream, to light green and light blue. On this medium isolated, hard masses of compacted, blue mycelium, of a sclerotial nature, are produced in considerable numbers. On oat extract agar growth is similar, but rather less luxuriant.

On slices of cooked potato tuber the mycelium produces a distinct blue colour in the medium, while the moist masses of the conidia on the surface are coloured distinctly light green. Chlamydospores are produced abundantly, and so are the blue sclerotium-like bodies already alluded to.

On cooked potato-stalks the growth is very similar. Chlamydospores are present, but the blue sclerotium-like bodies are not developed.

Influence of Light.—Our cultures were carried out in test tubes 15 cm. long, which for convenience sake were grouped in tens, and were placed in round tins about 8 cm. high. Even when standing in the laboratory the amount of light which could reach the culture was therefore but small; and when, as was often the case, they were kept in a dark cupboard, light was, of course, totally excluded. Under these circumstances, the substratum and mycelium were as a general rule of a more or less indigo blue colour, while the superficial moist conidial masses were coloured light green.

Parallel cultures were carried out in light and in darkness to ascertain what influence (if any) light had on the coloration produced. The cultures were kept in a window facing north, so that they were not exposed to direct sunlight. One half of them were fully exposed and the other half were carefully covered with thick black paper in such a way as to exclude all

[1] For the method of preparing these media see Sci. Proc. Roy. Dublin Society, xiii, (N.S.). No. 36. March 1913, p. 578 and p. 580.

light. The inoculum used in each case consisted of a portion of a green, moist mass of conidia, together with a small amount of adhering mycelium.

The experiment lasted forty days. In the dark the conidial masses were, as a rule, of the greenish blue colour already familiar to us, with occasionally some which were white or dirty white in colour. In the light, however, the conidial masses were of a "bitter-sweet pink" (Ridgeway) colour.

Influence of Moisture.—This experiment was repeated in a slightly modified form. Not only were the cultures divided between light and darkness, but the effect of an abundant and of a restricted amount of moisture was studied at the same time. With regard to the latter, no effect was observable as far as development of colour was concerned, but the extra moisture merely led to a more luxuriant growth of the culture. As in the previous experiment, however, it was found that the presence of light caused the development of the bitter-sweet pink colour in the masses of conidia, while in the absence of it they were light green. It has already been pointed out that the fungus pustules present on rotting tubers become pink in colour when exposed to a good light.

Appel and Wollenweber describe the pure colour of the conidia of *F. cæruleum* as being reddish-ochre when grown in bright daylight, but brownish white with a minimum of light. The verdigris-green colour often observed in the conidial masses is regarded by these authors as being a mixture of the brownish-white of the conidia with the indigo blue of the substratum. We, however, were not able to confirm this.

Nature of the Colouring Matter.—If a portion of a culture in which the blue colour is well developed (as, for instance, one on cooked potato) be boiled in water, no extraction takes place. The colour, however, is extracted by dilute hydrochloric acid in the cold, and it at once changes to pink. The addition of an alkali to the pink solution causes it to become blue.

Influence of Acid or Alkaline Reaction of Media.—Cultures were carried out on media, made both distinctly alkaline and distinctly acid, and in the former case the colour developed was deep blue. In the acid medium the fungus grew satisfactorily, but the colour first produced was of a wine-red tint. Subsequently, when the acidity of the medium had become neutralized by the alkalinity, developed as the result of the growth of the fungus, the colour changed to blue. It may be remarked here that the juice expressed from the diseased portion of an affected tuber gives an alkaline reaction to litmus, while the normal juice of a healthy tuber is, of course, slightly acid.

Proofs of Pathogenicity.—A large number of experiments involving the inoculation of healthy potato tubers with the various strains of the fungus

were made. Into the exact details of all of these space does not permit us to enter, and a general account of them must suffice.

In every infection experiment undertaken controls were used, consisting of tubers similar to those used for inoculation, and treated similarly to the latter, except that no actual inoculation of them was made. In every case these control tubers remained sound and free from rot.

The general method adopted for practically all of the inoculation experiments consisted, first, in carefully selecting healthy tubers with undamaged skins. These were then well washed in water, and next steeped for a short time in a weak solution of formaldehyde. Finally, they were washed in sterile water and then allowed to dry. The inoculating material was introduced through wounds specially made with a sterile scalpel. A more or less tetrahedral or conical cut was made into the tuber, and the cone of tissue, still attached by a small portion of skin at its base, was everted. The inoculum was placed in the bottom of the cavity thus produced; the apex of the cone cut off and its base closed down on the inoculum. By this means a gaping wound was avoided, and the chance of contamination from stray spores minimized.

A positive result was only regarded as having been obtained when the rot produced was extensive and progressive. In such cases the whole tuber ultimately became rotten, if kept long enough. Cases where a certain amount of rot at first proceeded from the inoculation wound, but did not progress further owing to the formation of a layer of cork cutting off the infected area, were regarded as negative.

The inoculated tubers were kept in covered glass dishes, at least for a short period after the inoculation had been made, at laboratory temperatures. Later on the lids were sometimes removed, and, when once the rot had definitely started, its rate of progress did not appear to be affected in any very marked degree by varying conditions of dryness or moisture.

Out of a total of 848 inoculated tubers there resulted in 577 cases (i.e. sixty-eight per cent. of them) complete rotting of the tubers. The failure to cause rot was sometimes due to non-maturity of the tubers used, or to the variety used being more or less resistant. In the total mentioned we have included all the trials made, and these factors are of considerable importance in deciding whether infection will occur or not. One hunded and eighty-two tubers were inoculated at various times with the strain of *F. cæruleum* obtained from Amsterdam, and in eighty-four of them (i.e. forty-six per cent.) the typical rot was produced.

It was not considered necessary in more than a few cases to complete the detailed proof that the fungus used for inoculation purposes was in reality the

cause of the rot by isolating it again from the decaying tubers. This was, however, done in six cases, and the fungus obtained in pure culture in each case.

Pathogenicity towards Plants other than the Potato.—Attempts were made to infect onions, mangels, carrots, parsnips, and apples with pure cultures of *F. cæruleum*; but the fungus proved itself to be non-pathogenic in these cases, at least under the conditions of the experiments, which were similar to those under which positive results were obtained with potato tubers.

Similar trials were made with tomato fruits, the fungus being inoculated through wounds made for the purpose. In both of two sets of experiments positive results were obtained. The decay produced in the fruit is not particularly rapid, only about one quarter of the inoculated fruit becoming involved during the course of a fortnight.

The surface of the decayed area becomes somewhat sunken and covered with a layer of conidiophores bearing conidia which, in the mass, are of a pinkish-cream colour. Cavities occur in the decayed tissue of the fruit, which are more or less completely filled with white mycelium. The decayed tissue is of a spongy consistency, and is thoroughly permeated with mycelium.

From small portions of such diseased tissue, removed under aseptic conditions and placed upon suitable media, the fungus was re-isolated in pure culture, thus completing the proof that it was the cause of the decay. Control fruits treated similarly to the inoculated ones, but not inoculated, remained perfectly healthy.

It is clear, therefore, that this fungus is pathogenic to the fruits of the tomato provided wounds are present. Whether it can attack the uninjured fruit or not we are not in a position to say.

Influence of Maturity of the Tuber on the Susceptibility to Infection.—Some of our infection experiments were made in the summer and early autumn, and the results were more or less negative. Further trials soon aroused the suspicion that the age or maturity of the tubers had a considerable influence on the susceptibility to infection, and specific experiments were, therefore carried out to ascertain whether the suspicion was well-founded or not.

For this purpose tubers of the varieties "May Queen" and "Ninety-fold," known to be susceptible, were used. It was found that one of the strains of *F. cæruleum* when inoculated in the early summer into May Queen tubers of the previous season produced dry-rot with ease and certainty, but that when the same strain was used to inoculate tubers of the same variety newly dug in July, the results were almost entirely negative. Hence a series of periodic inoculations was carried out, the details and results of which are summarized in the following table. The tubers used were specially grown

for the purpose and the same stock used throughout the trials. In addition to one of our own strains of *F. cæruleum* we also used the one obtained from Amsterdam for inoculating purposes, this being done through wounds as already described for other such experiments. Controls were of course used in all cases, and in every instance they remained sound.

Inoculated with		*F. cæruleum* (own strain).		*F. cæruleum* (Amsterdam strain).	
Variety of Tuber.	Dates of Inoculations.	No. of Inoculations.	No. of Rots.	No. of Inoculations.	No. of Rots.
May Queen	July 31, 1915	20	1	20	1
	Oct. 22, ,,	10	2	10	1
	Nov. 22, ,,	20	7	20	9
	Dec. 22, ,,	20	15	20	13
	Jan. 22, 1916	20	16	20	17
	Feb. 22, ,,	20	20	20	20
Ninety-fold	Sept. 8, 1915	20	0	20	0
	Oct. 22, ,,	10	7	10	0
	Nov. 22, ,,	20	17	20	9
	Dec. 22, ,,	20	16	20	12
	Jan. 22, 1916	20	20	20	15

The table clearly shows that there is a progressive susceptibility to rot, the maximum being reached early in the new year. This fact probably explains why it is that complaints of serious losses due to dry-rot are not made as a rule until some months after storage has begun.

The cause of the increased susceptibility is perhaps to be looked for in some change in the chemical composition of the contents of cells of the tuber, and with this in view, an attempt was made to increase the susceptibility to decay in autumn by keeping the tubers for some twenty hours or so in a vessel surrounded with a mixture of ice and salt before inoculation. This treatment was so arranged as not to be severe enough to kill the tubers by freezing, and they sprouted quite normally subsequently. It was found, however, that the tubers were not thus rendered more susceptible to infection. Two experiments of this kind were carried out, and when the

second gave negative results like the first the matter was not pursued further. It was thought that possibly the development of sugar was the factor which influenced infection, but the matter does not appear to admit of so simple an explanation.

Varieties naturally resistant to Infection.—Seeing that dry-rot is more frequently met with in some varieties than in others, it is natural to suppose that certain of them are more resistant than others, and that some may even be quite immune.

Two series of infection tests were carried out with nine varieties of early potatoes raised for the purpose at the temporary phytopathological station at Clifden, Co. Galway.

The inoculations were made as previously described, and the culture used was one which produced one hundred per cent. of rots in inoculations of tubers of "May Queen" just previous to the experiment. Ten inoculations were made in each case, and the results are summarized in the following table—

Variety of Tuber.	No. of cases of Rot in	
	Series I.	Series II.
Ninety-fold, . .	10	10
Early Puritan, . .	10	10
Sharpe's Express, . .	8	10
May Queen, . .	8	10
Duke of York, . .	6	10
Midlothian Early, . .	4	10
Eclipse, . .	6	7
Windsor Castle, . .	3	4
Epicure, . .	0	2

The results point to the conclusion that at least the varieties Eclipse, Windsor Castle, and Epicure, are less susceptible to attack than the other varieties; and they suggest that a systematic trial of the pathogenicity of the fungus towards an extended list of varieties might yield important economic results.

Since liability to infection is influenced both by the variety of the tubers used and by their degree of maturity, it follows that in any studies as to the

pathogenicity of members of the genus Fusarium towards the potato cognisance must, as has already been explained, be taken of these factors. Possibly some of the conflicting results obtained by earlier workers may be accounted for by failure to appreciate the significance of these factors, although perhaps it is just as likely that in some cases the species under investigation by the different authors were not really identical.

How Tubers become Infected.—Attention has already been called to the fact that naturally infected tubers frequently exhibit wounds from which, it is fairly clear, infection started. Seed potatoes are frequently transported in sacks and, under the conditions of transit, the tubers are exposed to a good deal of bruising. Such bruising frequently results in small cracks being produced in the skin. It was proved by experiments with three varieties of potato that the fungus could infect the tubers through wounds deliberately produced by bruising and thus cause the rot; and it is believed that bruising in transit may well be an important factor leading to infection.

It was also proved that the wounds resulting from the breaking off of the young shoots from sprouted tubers formed very favourable points of entrance for the fungus. The careless handling and planting of sprouted tubers often results in some of the sprouts being broken off. Some of the cases in which presumably healthy seed-tubers have been observed to decay from dry-rot in the ground after planting may probably be explained by the entry of the fungus through wounds of this kind.

Infection experiments were also carried out with tubers which, so far as careful examination with a good lens could disclose, had perfectly intact skins. In one case infection occurred at an eye, and in several cases at lenticels. Since these results were somewhat unexpected, the experiments were extended. Nine specially selected tubers of the Variety Early Puritan, which, except for a few small scab spots, had perfectly intact skins, were carefully washed in sterile water and allowed to dry. Some of them were unsprouted and some had sprouts about 5mm. long. They were not treated with any disinfectant, for fear of causing any damage to the eyes or the sprouts. Five of these tubers were then steeped for a few seconds in a suspension of the spores of *F. cæruleum* in sterile water, while the remaining four were steeped for the same length of time in sterile water alone.

Both lots were then kept in a moist atmosphere in covered glass dishes at laboratory temperature. The four tubers which were steeped in sterile water remained absolutely free from any kind of rot. Dry-rot was set up, however, in a short time at many points in the five tubers steeped in the spore suspension. Ten cases of infection through scab spots and lenticels were noticed, while infection occurred also in six cases through unsprouted

and uninjured eyes. In one case a sprout of about 1 cm. long became infected at its uninjured tip, and the fungus passed back through this sprout, killing it, and eventually reaching the tissue of the tuber. In five other cases sprouts became similarly infected, but at the conclusion of the experiment the decay had not extended from them to the tuber.

It is, therefore, clear that although this fungus is, perhaps, most frequently a wound-parasite, yet, under favourable conditions, it can attack uninjured tubers through lenticels, eyes, or young sprouts.

Results of Planting Infected Tubers.—Nearly every season we have brought to our notice one or more cases where early potatoes have failed to make a stand, or have made only a very bad one. Almost invariably these have been cases in which cut sets were planted, which were found when dug up to be seriously decayed with dry-rot. In such cases of course it is impossible to say after the event whether the seed tubers used were at fault, or whether the sets became infected from the soil, subsequent to planting.

In order to ascertain what happens when naturally infected whole tubers are planted, nine such tubers, ascertained to be infected with *F. cæruleum*, were planted in pots of soil in an unheated greenhouse. Healthy tubers were planted in pots of similar soil for purposes of comparison. Three of the infected tubers rotted completely in the soil and gave rise to no plants. The other six produced small plants, which remained perfectly healthy, died off eventually in a natural way, and in *post-mortem* examination showed no evidence of attack by *F. cæruleum*, or other organism.

Four tubers artificially inoculated with the fungus were also planted after the rot had become well established. All four produced small, healthy plants, which died off naturally, and no traces of the fungus could be found in them on subsequent microscopical examination.

It is our experience that if, when planted, a tuber is already seriously decayed with dry-rot, and particularly if the decay is in close proximity to the eyes or sprouts, the probability is that no plant will be produced. If, however, when the tuber is planted the amount of decay is slight, or is not in the immediate neighbourhood of the eyes or sprouts, the latter have time to grow and produce overground shoots having their own roots; and these shoots do not subsequently become invaded by the fungus.

Does F. cæruleum cause a Disease of the Potato Plant as a whole, or only a Rot of the Tuber?—If this fungus were capable of attacking the roots of the potato plant, and of thus killing it, we should have expected this to happen when either naturally or artificially infected tubers were planted. It would seem almost certain that under such conditions the roots on the underground portions of the stalks would be exposed to infection by contact with the

decaying tubers themselves. Since, however, as described above, the plants produced from diseased tubers remained healthy, we conclude that the fungus is not capable of attacking the roots.

Experiments were made to ascertain whether *F. cæruleum* is capable (like *Verticillium albo-atrum*) of producing hadromycosis, that is, of growing in and choking up the wood vessels, and thus causing a type of "wilt" disease.

As a result of several preliminary trials it was found that this fungus refused to grow on freshly cut, living portions of potato stalks, whether inoculated on the freshly-cut surfaces, on the uninjured surface, or even into freshly-made wounds in such stalks. These trials were made with portions of stalks a few centimetres long, from which the leaves were removed, and which were kept moist in test tubes provided with cotton-wool plugs.

Further trials were next made by inoculating the fungus into rather deep wounds, traversing all the tissues, made in various regions of the stems of leafy stalks cut from the parent plant, and kept with their cut ends in water. By occasionally changing the water and renewing the cut surface at the base of the stalk such leafy shoots, if kept in a good light, will remain in good condition, and continue to grow for some weeks. Uninoculated cut shoots were, of course, also kept under similar conditions for purposes of comparison and control.

The results of these trials were entirely negative. After four weeks the inoculated stalks showed no signs of wilting, and microscopical examination of the tissues showed that there had been no extension of the fungus from the inoculation wound either in the cavities of the wood-vessels or elsewhere.

The inoculation of plants growing in pots was then proceeded with, three series of experiments being made. In the first series the stalks, when about twenty centimetres high, were inoculated (under as aseptic conditions as possible) just below soil level, the wound being made at a node. After inoculation the wounds were bound up with tinfoil, and the disturbed soil replaced. Inoculation with *Verticillium albo-atrum* in this manner invariably results in causing a wilt disease of the plant, but in no case did this happen with *F. cæruleum*.

One of the six inoculated plants did, it is true, die prematurely, but this, it is believed, was due to the effects of a somewhat drastic fumigation rendered necessary by an attack of aphides from which both the inoculated and control plants temporarily suffered. The dead plant was thoroughly examined microscopically, but no mycelium was found in the stem except at the inoculation wound from which no spread had occurred. The same was

found to be the case with the other inoculated plants which remained healthy, and were microscopically examined three months after the inoculations were made. The controls behaved in a similar manner.

The second series of inoculations was a repetition of the first. Eight healthy plants were inoculated as in the previous series. They remained healthy, except in one case, and after a period of two months they were subjected to microscopical examination. The seven plants showed no traces of the fungus in them, except immediately at the inoculation wound, from which it had not spread. The eighth plant died after the expiration of one month. Mycelium was found in its vessels, but this, as the result of cultural trial, was found to be *Verticillium albo-atrum*. Examination of the undecayed parent tuber showed that this fungus was also present in it; and there can be little doubt but that this tuber was infected with Verticillium before it was planted.

In the third series the tubers selected for use were first carefully tested to make sure Verticillium was not present in them. The Verticillium-free tubers were then allowed to sprout, and when the sprouts were from two to three centimetres long, one main sprout on each was inoculated with *F. cæruleum*, through a wound made for the purpose. The other sprouts and eyes were removed. The tubers were planted, and all six of them produced perfectly healthy plants, as also did four tubers (not inoculated in the sprouts) used as controls. The stalks were subjected to microscopical examination, but no mycelium was found in their wood vessels. The newly-produced tubers were also examined, and found not to be invaded at their heel-ends by any fungus.

As a result of these experiments we conclude that *F. cæruleum* does not cause a wilt disease of the plant, and in this respect it appears to differ from *F. oxysporum* and *F. trichothecioides.*

Control of Dry Rot.—Our experience with this disease is that when once a tuber begins to rot it is practically impossible to effect a cure. From twenty naturally affected tubers the diseased portions (which were then comparatively small) were very carefully cut out on December 19th, 1913. Flowers of sulphur was then thoroughly rubbed into the wounds. After two months, however, nineteen of these tubers had completely rotted. Either the whole of the diseased tissue had not been cut out originally, in spite of the care exercised, or re-infection from spores had then or subsequently occurred, and this in spite of the presence of sulphur.

Ten healthy tubers (variety Windsor Castle) were washed and dried. Five were then inoculated with *F. cæruleum* through wounds as previously described. Just before the other five were quite dry they were rolled in

flowers of sulphur. They were then wounded, and into the wounds flowers of sulphur was thoroughly rubbed. Finally, *F. cæruleum* was inoculated into the sulphured wounds.

Both lots of tubers were kept under the same conditions at laboratory temperature, and were examined at the end of a month. It was then found that the rot had become thoroughly established in all ten tubers, and that the presence of the sulphur had exercised no influence either in preventing infection or in retarding decay. Hence the use of sulphur for the control of this rot as suggested by Massee[1] cannot be recommended. A similar experiment was carried out using slaked lime in the place of sulphur, and the result was identical.

It might be expected that at low temperatures the rot would be inhibited. Yet it must not be forgotten that it proceeds in potato pits and stores during the winter months when the temperatures in them certainly cannot be high. It was found that tubers artificially inoculated with the fungus and kept in an unheated greenhouse, where the temperature varied from 0°C. to 6°C. during the nights, and on some occasions rose to a maximum of 25°C. during a portion of the day, became infected quite as easily and rotted quite as rapidly as others inoculated at the same time and kept in an incubator at a constant temperature of 20°C., while a similar lot inoculated and kept at 30°C. remained quite free from infection. It is doubtful, therefore, whether keeping tubers at an unusually low temperature, even if this could be managed in practice, would be a successful method of control, and it is by no means certain that such treatment would be good for the tubers themselves.

Affected tubers should certainly not be used for seed, for they give either no produce or only a poor "stand." Cutting sets from affected seed tubers and planting them is likely to lead to disastrous results, and this should be avoided.

In the raising and subsequent handling of potatoes care should be taken not to bruise or wound them, particularly if they are intended for seed purposes. This applies with special force to some of the early varieties, which have comparatively thin skins, and are often raised before they are thoroughly ripe, when the skins are peculiarly liable to abrasion and other injury. Care should also be taken when planting sprouted potatoes to avoid breaking off the sprouts. The practice of deliberately breaking off the sprouts to induce the growth of a further set is one which is to be condemned from all points of view.

"Prevention is better than cure," but seeing that we do not yet really

[1] Diseases of Cultivated Plants and Trees, p. 183.

know for certain the source from which the infection primarily comes, it is not easy to suggest preventive measures. Presumably the fungus is a normal inhabitant of the soil, but research on this point is much needed.

Other Species of Fusarium. F. arthrosporioides, &c.—In addition to isolating and cultivating the various strains of *F. cæruleum* as described above, a very considerable amount of time has also been devoted to the study of other species of Fusarium, principally *F. Solani* (Mart. pro parte) A. & W., *F. Martii* A. & W., *F. discolor* A. & W. var. *sulphureum* (Schlecht.) A. & W., and *F. trichothecioides* A. & W. Strains of the first three species were obtained from the Central Bureau in Amsterdam, while the fourth was kindly supplied by the U.S.A. Bureau of Plant Industry.

In some respects *F. Solani* and *F. Martii* resemble *F. cæruleum*, but they both differ from the latter in the essential point that they are non-pathogenic to the potato tuber. We were unable in spite of repeated trials to produce a rot in tubers by inoculating with *F. discolor* var. *sulphureum*—a species which other authors have found to be pathogenic to potatoes. Possibly the strain used had lost its pathogenic character, owing to prolonged saprophytic culture.

With *F. trichothecioides*, however, a dry-rot of potato tubers was readily produced. The form of rot caused by this fungus is somewhat different from that caused by *F. cæruleum*. Characteristic of the *cæruleum*-rot is the presence of comparatively few internal cavities which contain mycelium often of a blue colour and relatively few conidia. The pustules which break through the skin are compact and firm, and are blue at their bases. There is a faint but pleasantly aromatic odour in the decaying tubers. In the case of *trichothecioides*-rot the attacked tissues are at first more spongy, owing to the considerable development of cavities. The mycelium in these cavities is never blue, and it bears an abundance of conidia. The external pustules are more loose in texture, and there is no aromatic odour. These differences, however, with the exception perhaps of the presence or absence of the blue colouring matter, are scarcely well marked enough to make a differentiation between the two kinds of rot an easy matter without having resort to cultures.

During the past three or four years in which our attention has been specially directed to the matter we have never seen a case of natural dry-rot in the potato tuber produced by any species of Fusarium other than *F. cæruleum*, but further study and experience may possibly bring such to light. We have, however, found at least one other species in this country which has proved, on trial, to be pathogenic to potato tubers. A tuber of an

early variety partially affected with "blight" (*Phytophthora infestans*) was lying, still attached to the parent plant, with part of its surface exposed. On this surface were two pinkish pustules made up largely of Fusarium conidia. These conidia were mainly 5-septate and measured on the average $40\mu \times 4\mu$. From a conidium a pure culture of the fungus was obtained.

Inoculations into healthy tubers with this pure culture caused dry-rot to occur in them, rather less readily in the month of November than in February, when the rot occurred in all the cases tried (twenty-nine altogether). That the fungus inoculated into the tubers was responsible for the rot was proved by re-isolating it in pure culture from one of the rotted tubers. The halves of a tuber inoculated at each end with this species, and cut longitudinally after the rot had become established, are shown in fig. 5, Plate VI.

An extended series of cultures was made of this species on various media, but it is not proposed to go into details concerning them here. It may be stated, however, that the colour of the conidial masses produced on sterilized potato stems varied from buff-pink[1] to pinkish cinnamon. On some media, such as Quaker Oat agar and oat extract agar, it was noted that the production of masses of conidia (pseudo-pionnotes) was accelerated by pushing aside the aerial mycelium and thus exposing the surface of the medium. No chlamydospores were observed in cultures on any of the media used.

Characteristic of the fungus when growing on several media was the production of a surface layer of a colour varying from "spinel-red" to "pansy-purple." When the medium was made acid this colour became yellow, like honey, but when made alkaline it turned reddish-purple.

A culture on cooked potato was boiled with dilute caustic potash solution and filtered, when a claret-coloured filtrate was obtained. On acidifying and again filtering, a honey-yellow filtrate was obtained. This filtrate made alkaline again returned to the original claret-colour. These colour-changes are therefore quite different from those described in the case of *F. cæruleum*.

From a study of its morphological and cultural characters we believe that this fungus is identical with *Fusarium arthrosporioides* Sherb., so that this species must now be regarded as pathogenic to the potato tuber. It is interesting to note that Sherbakoff gives as the habitat of this species "In discoloured tissues of tuber of *Solanum tuberosum*, Ireland." We have only met with this species once, and only on a single tuber, and it was not clear

[1] The colours mentioned here are named according to Ridgeway's "Color Standards and Color Nomenclature." 1912.

whether it or *Phytophthora infestans* was the more responsible for the decay of the tuber on which it was found. It certainly is not the cause of our common dry-rot, but the possibility that it may occasionally be a cause of dry-rot must not be overlooked.

IV.—Conclusion.

The dry-rot of the potato tuber which commonly occurs in the British Isles is due to the attacks of *Fusarium cæruleum* (Lib.) Sacc. The two species, *F. oxysporum* Schlecht. and *F. trichothecioides* Woll., which are largely responsible for a somewhat similar type of rot in certain parts of the United States of America, have not been met with in this connexion up to the present in the British Isles.

On a single occasion *F. arthrosporioides* Sherb. was met with and was proved to be capable of causing a dry-rot of the potato tuber. Further research may perhaps show that this and possibly some other species of Fusarium are occasionally responsible for the production of dry-rot here.

F. cæruleum does not produce hadromycosis of the potato plant, nor does it kill the plant by attacking the roots. It can destroy tomato fruits, but does not attack onions, mangels, carrots, parsnips, or apples.

Infection frequently occurs through mechanical wounds such as those caused by implements, by bruising, and by breaking off the sprouts. It may also occur through scab spots. Wounds, however, are not essential, for infection can take place through the lenticels, eyes, or young sprouts of uninjured tubers.

Potatoes become more susceptible to infection as they become more mature, hence the rot is more prevalent during the later than during the earlier period of storage. Some varieties of potatoes are more resistant to infection than others.

Affected tubers cannot be cured, and the application of sulphur or lime for preventing infection or retarding the rot is of no practical value.

V.—Explanation of Plates.

Plate VI.

Fig.

1. A tuber naturally infected with *Fusarium cæruleum* at a comparatively early stage of dry-rot, showing the characteristic shrinking and wrinkling of the skin over the affected portion, and the white conidia-bearing pustules of the fungus breaking through. (December, 1916.)

2. A naturally infected tuber in the last stages of dry-rot. Having been exposed in a window to a good light, the numerous fungus pustules were pinkish in colour. The tuber was much shrunken, dry, light in weight, and very hard. Infection, in all probability, occurred at the wound visible in the centre. (April, 1916.)

3. Four tubers artificially inoculated through wounds with a pure culture of *F. cæruleum*. In the case of the two upper tubers the rot had been in progress for nine, and in the lower two for four and a half, weeks at the time when the photograph was taken. (November, 1914.)

4. Four tubers ten weeks after being inoculated with a pure culture of *F. cæruleum* by applying it to the skins after scratching them. (January, 1915.)

5. The two halves of a tuber five weeks after having been inoculated with *F. arthrosporioides* through two wounds on the upper surface, one near each end. (March, 1916.)

Plate VII.

1. A branched conidiophore of *F. cæruleum*, from a 26-days old culture on Quaker Oat agar, showing the "collar" at the extremity of each sterigma except the one on the left to which a young conidium is attached. (× 500.)

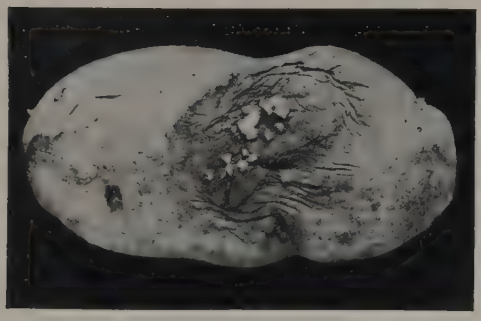
Fig.

2. Typical conidia of *F. cæruleum* from a culture on oat-extract agar. (× 840.)

3. Conidium from a 21-days old culture of *F. cæruleum* on oat-extract agar, germinating after five hours in a hanging drop of water at laboratory temperature.

4. Chlamydospores of *F. cæruleum* from a culture on oat-extract agar. (× 840.)

5. Chlamydospores of *F. cæruleum* germinating. (× 840.)



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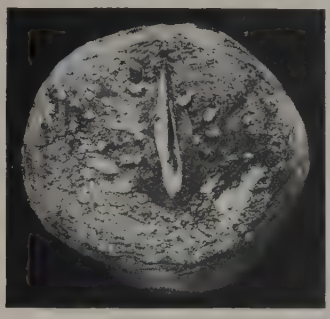

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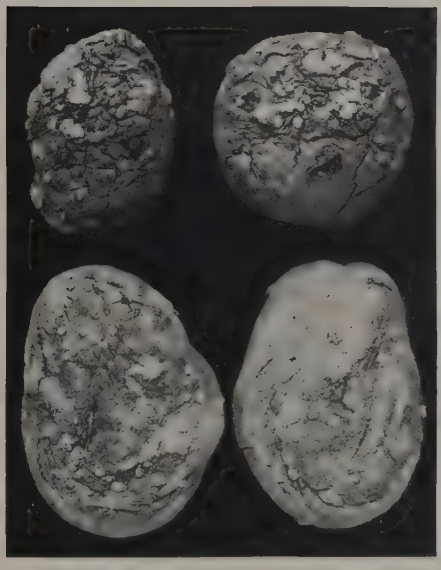

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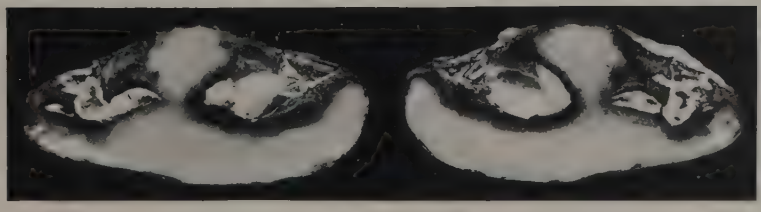

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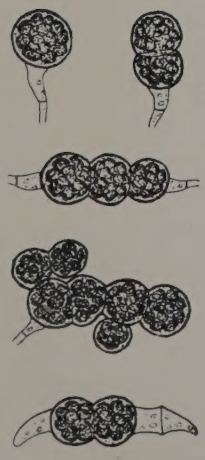

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